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Vegetation classification and ordination of the central Hamersley Ranges, Western Australia

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Abstract

Vegetation studies of Australian mountainous deserts are limited. The Hamersley Ranges region of north-west Australia is such an environment. It comprises a series of ranges and other uplands which rise above an extensive plateau. Geologically the region is complex (bedrocks range from Archaean granites & gneisses to Proterozoic sedimentary ironstones to Tertiary limestone to various colluvial and alluvial deposits). At 139 sites within the central portion of the Ranges, the cover, frequency and abundance of perennial plant species were measured. The data were used to construct a site dissimilarity matrix using the Bray-Curtis measure. Both hierarchical (flexible-UPGMA) and non-hierarchical (ALOC) classification procedures were used on this matrix to derive a vegetation classification consisting of 16 plant communities, 2 vegetation types and 8 sub-types. Each community is described in detail and contrasted in terms of floristics, life-forms, structure and indicator species. Ordination (using a hybrid form of multidimensional scaling) showed intergradation of communities in terms of species composition, although the lowland communities were found to be relatively distinct from the uplands and pediment slopes. A floristic gradient along the topographic profile from mountain/hill top to valley floor was identified in the ordination space and characterised in terms of dominant species. A differential profile constructed for such floristic gradient found that, spatially, the transition zones between communities varied in width and other characteristics. It is hoped that the classification scheme and the methodology developed here will serve as a foundation for the whole Hamersley Ranges region.

Keywords: vegetation, plant communities, classification, arid climate, Pilbara, Hamersley Ranges

Introduction

Extensive areas of hot desert with mountainous terrain are found on all continents with the exception of Antarctica and Europe (Evenari *et al.* 1985). Plant communities and other vegetation types have been determined and described for a large number of such areas (Goodall & Perry 1981; Evenari *et al.* 1985). Although they have employed a variety of classification approaches, such studies have regularly demonstrated or described the distinctiveness of plant communities, both spatially and in terms of species composition. Such vegetation patterning has often been attributed to the distinctiveness of landforms in such regions (Ayyad 1981; Wierenga *et al.* 1987; Abbas *et al.* 1991; Cowlishaw & Davies 1997). For instance, typical desert landforms, such as hill slopes, pediments, bajadas, playas and regs, are often reported as having characteristic plant communities with relatively sharp boundaries between communities. Other authors have shown that, although some landforms have characteristic communities and dominant species, measurable gradients in species composition occur in the landscape in response to environmental gradients linked to gradually decreasing slopes and/or altitude (Ezcurra *et al.* 1987; Cornelius *et al.* 1991; Ghazanfar 1991; Parker 1991; Vetaas 1992; Patten & Ellis 1995). This often results in broad transition zones between communities (i.e. ecoclines), especially along subdued slopes of the piedmont ("foot of the mountain") zone. Where vegetation studies have been regional rather than local in extent, various geological substrates and climatic gradients are likely to be encountered, which further complicates variation patterns. There are some reports of different communities on the same landform in response to different types of parent rocks (Danin & Orshan 1990; Ward *et al.* 1993), whilst others have reported geological control on vegetation to be secondary to landform (Parker 1991).

Mountainous deserts cover about 12% of Australia's extensive arid zone (Mabutt 1977; Williams & Calaby 1985). They are generally of much lower relief than mountainous deserts elsewhere, but tend to show the same broad pattern of landforms. Examples include the Macdonnell, Flinders, Central and Hamersley Ranges. The Hamersley Ranges cover an extensive area of approximately 60 000 km^2 within the arid, north-west of Australia (Fig 1). The Ranges consist of a series of east-west trending mountain ranges rising above an extensive plateau. Between the ranges are broad drainage systems. Previous vegetation studies of the Ranges are limited and comprise a regional delineation and mapping of "communities" at a broad (1:1 000 000) map scale (Beard 1975) and several local, fine-scale studies of areas subject to mining developments, typically around 100 km^2 in extent (e.g. Trudgen & Casson 1998). Between these two extremes in scale, vegetation descriptions are absent. Furthermore, it is common for vegetation units in such studies to be defined subjectively and on the basis of physiognomy and dominant species, rather than overall floristic differences. This paper aims to fill this void by determining and describing vegetation types and communities in the central portion of the Hamersley Ranges using floristic data and multivariate methods. The degree to which vegetation units are floristically and spatially distinct will also be addressed. It is hoped that the vegetation classification and the methodology established here will form the basis for a classification scheme for the whole Hamersley Ranges region. Such a classification scheme would be of considerable benefit to those involved in conservation planning and impact assessment throughout the region, particularly as the amount of development is expected to increase dramatically over the next decade.

Methods

Study area

The study area was located within the central portion of the Hamersley Ranges some 1100 km north of Perth, and was approximately 120 x 80 km in size (Fig 1). The area is dominated by Karijini National Park and is situated between the towns of Newman, Tom Price and Wittenoom (Fig 1). The Hamersley Ranges are located on the Hamersley Plateau, an extensive area which gently rises from north of the Ashburton River and ends in a sharp escarpment at the Fortescue River floodplain. The plateau surface lies 600–700 m above sea level. A series of east to west trending ranges and associated hills and mountains rise above the plateau a further 200 to 600 m. Characteristic landforms of the region are similar to those of other mountainous deserts (Cooke *et al.* 1993) and include: 1) slopes of hills, ridges and mountains; 2) pediment slopes (slopes of sorted colluvium at the base of hills, ridges, etc.); 3) bajada slopes (coalesced alluvial fans below pediments); 4) alluvial flats and broad drainage lines; 5) confined streams and creeklines; and 6) cuesta (scarp and dip slope topography) (Lorimer 1991). The surface geology of the Ranges is dominated by ironstones on the uplands and, in the broad valley systems, various formations of colluvium and alluvium. Ironstones date from the lower Proterozoic era when layers of iron rich sediment are believed to have been deposited while the area was inundated by sea (Twidale & Campbell 1991). A number of ironstone formations occur in the Ranges and they typically alternate with layers of dolomite and shale. In addition to these sedimentary rocks, Archaean (basement) granites and gneiss are found, predominantly in the south of the study area. Volcanic intrusions (mainly dolerite sills) are also

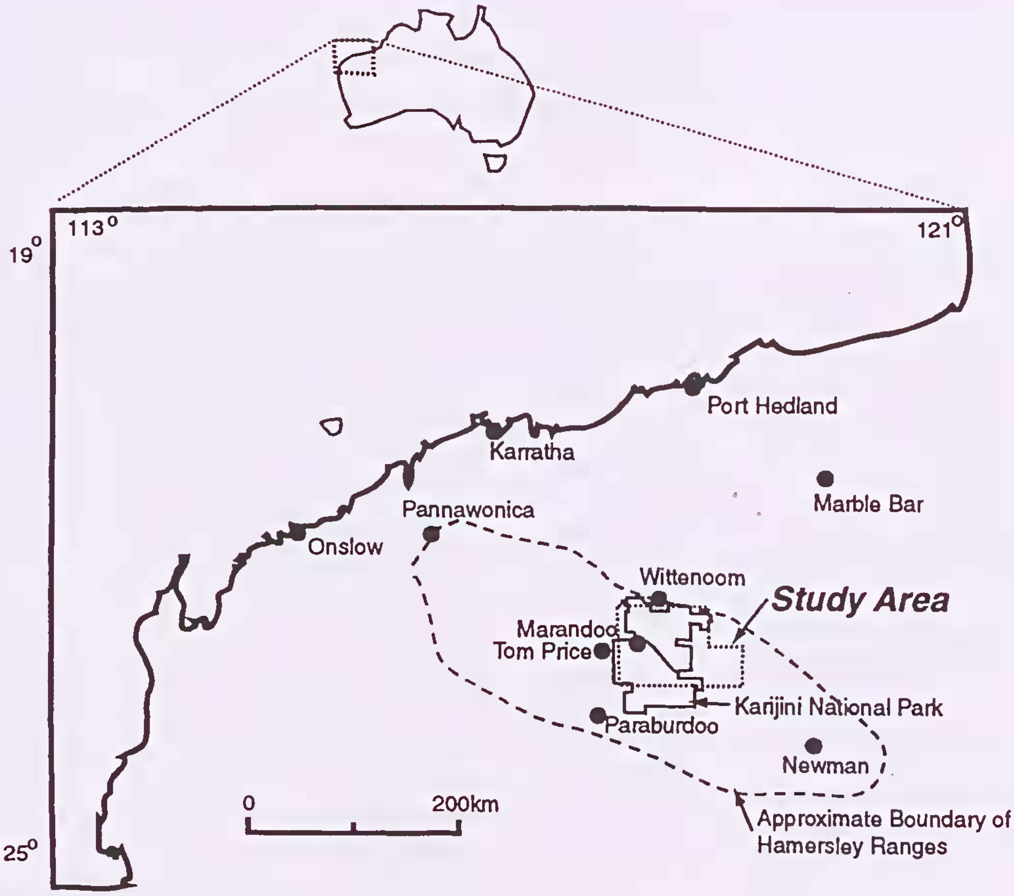

Figure 1. Location map showing the study area in relation to regional and State features.

found throughout the geological profile, particularly in the softer, dolomitic formations. The surface geology is therefore somewhat complex with the main geological formations of the study area surface being the Brockman Iron Formation, the older Marra Mamba Iron Formation, the Jerrinah Formation (very complex and dominated by dolomite and shale), the Weeli Wolli Formation (also dolomite and shale), Archaean granite, volcanics, Tertiary consolidated colluvium, the Oakover Formation (Tertiary calcareous gravels and limestone), Quaternary colluvium, and Quaternary alluvium (Thorne & Tyler 1997).

No long-term rainfall records are available for the study area. However, interpolation of long-term records from surrounding stations suggests rainfall for the study area is around 350 mm per annum on average (Beard 1975; van Etten 2000) and decreases in a southerly direction. This average figure however belies the very large temporal variability in rainfall across the region; the variability index of annual rainfall is between 1 and 1.2, which is classified as moderate to high (Bureau of Meteorology 1989). This variability mainly stems from the erratic nature of cyclonic rains during summer and autumn. In some years, cyclones cross the coast and bring large amounts of rain to the arid interior, whereas in other years no effective cyclonic rains may occur (Beard 1975). Winter rainfall averages around 40–50 mm, increases with distance south and is much more regular than summer rain. Temperatures and evaporation rates are high in summer with the mean January maximum close to 40°C. Winter maximum temperatures average around 24°C, with average minimum around 11°C. Mild frosts have regularly been observed during winter (Beard 1975), particularly in valleys and hollows.

Study sites & field measurements

Truly random selection of study sites was not possible given the lack of roads and tracks, the restrictions on off-road vehicle use and the ruggedness of the terrain. Alternatively, available roads and vehicle tracks were used to sample as much variation in landform type, geological substrate and altitude as possible. Altogether 139 sites were chosen for study. All major landform types and geological substrates were sampled several times throughout the study area. Areas immediately adjacent to roads were avoided because of the potential for edge effects, as were recently burnt areas given they have a suite of pioneer species. Sampling occurred over seven separate periods: June 1991, August 1991, December 1991, July 1993, December 1993, December 1994 and July 1995. The amount of rainfall before sampling, which influences annual and ephemeral species composition, varied considerably.

At each study site, a 20 m x 25 m plot was marked out on the ground and then divided into twenty 5 m x 5 m quadrats. This size plot (0.05 ha) was used as it has been recommended for studies of arid woodland communities (Fox 1981; Kent & Coker 1992) and supported by examination of species-area curves which showed they regularly capture the majority of species present at sites. In each 25m^2 quadrat, the abundance (number of individuals) and cover of each perennial species was estimated. Perennial species in this study included short-lived perennials (sometimes referred to as semi-perennials) which can survive longer than a year given favourable conditions. Most species of semi-perennials were present at all sampling times over the course of the study, although their abundance and the amount of green tissue varied somewhat. True annual species (i.e. those which consistently complete their life-cycles within a year) were not included in the analyses given their temporal variability. Species were identified using relevant keys and the W.A. Herbarium (Perth) collection with the authority for plant names and nomenclature being Paczkowska & Chapman (2000). Voucher specimens of all species collected are lodged in the Edith Cowan University Herbarium (Joondalup Campus).

Data analysis

An importance value (IV) was calculated for each perennial species at each plot by summing the relative cover, density and frequency of plants and multiplying by 100 (Curtis 1959). The sum of IVs for all species in a plot is 300. The IV of each species in the plot is therefore relative to the other species in the plot and is not an absolute measure. The main advantage of the importance value over other measures of cover/abundance is that it enables fair comparison of different sized plants. For instance a tree species (typically high cover, but low abundance) can have similar IVs to grasses/herbs/subshrubs (low cover, high abundance), but would differ considerably if either cover or abundance measures only were used. IVs were log transformed using the formula $x' = \log_e(x + 1)$ to downweight dominant species and to reduce the skewness of the data set – this effectively reduced the data to between 0.1 to 5. A site by species matrix was then constructed using transformed IVs and converted to a site X site dissimilarity matrix using the Bray-Curtis association measure (Bray & Curtis 1957) as recommended by Faith *et al.* (1987). Classification of sites was performed on the dissimilarity matrix using two different clustering strategies: ALOC (Belbin 1987) and flexible-UPGMA (Belbin *et al.* 1992). For the flexible version of UPGMA, b values of -0.1, as recommended by Belbin & McDonald (1993), were used. Ordination of the site dissimilarity matrix was performed using a hybrid multidimensional scaling method (SSH) with the "ratio-ordinal cut value" set at around 0.8 as suggested by locating a trough in the histogram of association values (Belbin 1991, 1994). In addition to ordination of all 139 sites, 35 sites located along a particular ridge-top to valley floor toposequence near Marandoo (Fig 1) were ordinated and a differential profile constructed by plotting the one-dimensional SSH scores against distance along topo-sequence (Hobbs 1986). Principal axis correlation (PCC) was used to calculate how well each species was linearly correlated to the ordination space and the direction of this correlation (Belbin 1994). To protect against spurious results using IV's, the same classification and ordination procedures were also undertaken using cover values (square root transformed) and compared to results using IV's.

Mean cover of all species and of various life-forms were compared for various vegetation units using one-way ANOVA, with Tukeys post-hoc test used to distinguish which pairs of means were significantly different. Means were first checked for equal variances and all cover values were arcsine transformed before analysis (Sokal & Rohlf 1981). Mean community species richness (of all species, as well as that of various life-forms), Shannon diversity index and evenness index (Kent & Coker 1992) were compared using Kruskal – Wallis test. Indicator species, defined as those species which characterise and differentiate a group, were determined for each community using the approach outlined by Dufrene & Legendre (1997). For each group of sites defined by the classifications, homogeneity (in terms of species composition) was calculated using the following formula: H=1-RV where *H* is the homogeneity and *RV* is the relative variance of a particular group and was calculated, following the recommendations of Pressey & Bedward (1991), using the dissimilarity measure used to construct the site X site association matrix. Simply, RV for a particular group was calculated as the average within-group association (i.e. of all pair-wise combinations of sites) divided by the average pair-wise association for the data set as a whole.

Results

Classification and descriptions of communities

The dendrogram resulting from the UPGMA classification of sites (Fig 2) was produced by first cutting the classification at the 21 group level and then joining 5 smaller groups (consisting of 1 or 2 sites) to adjacent groups in the dendrogram. This produced 16 groups,

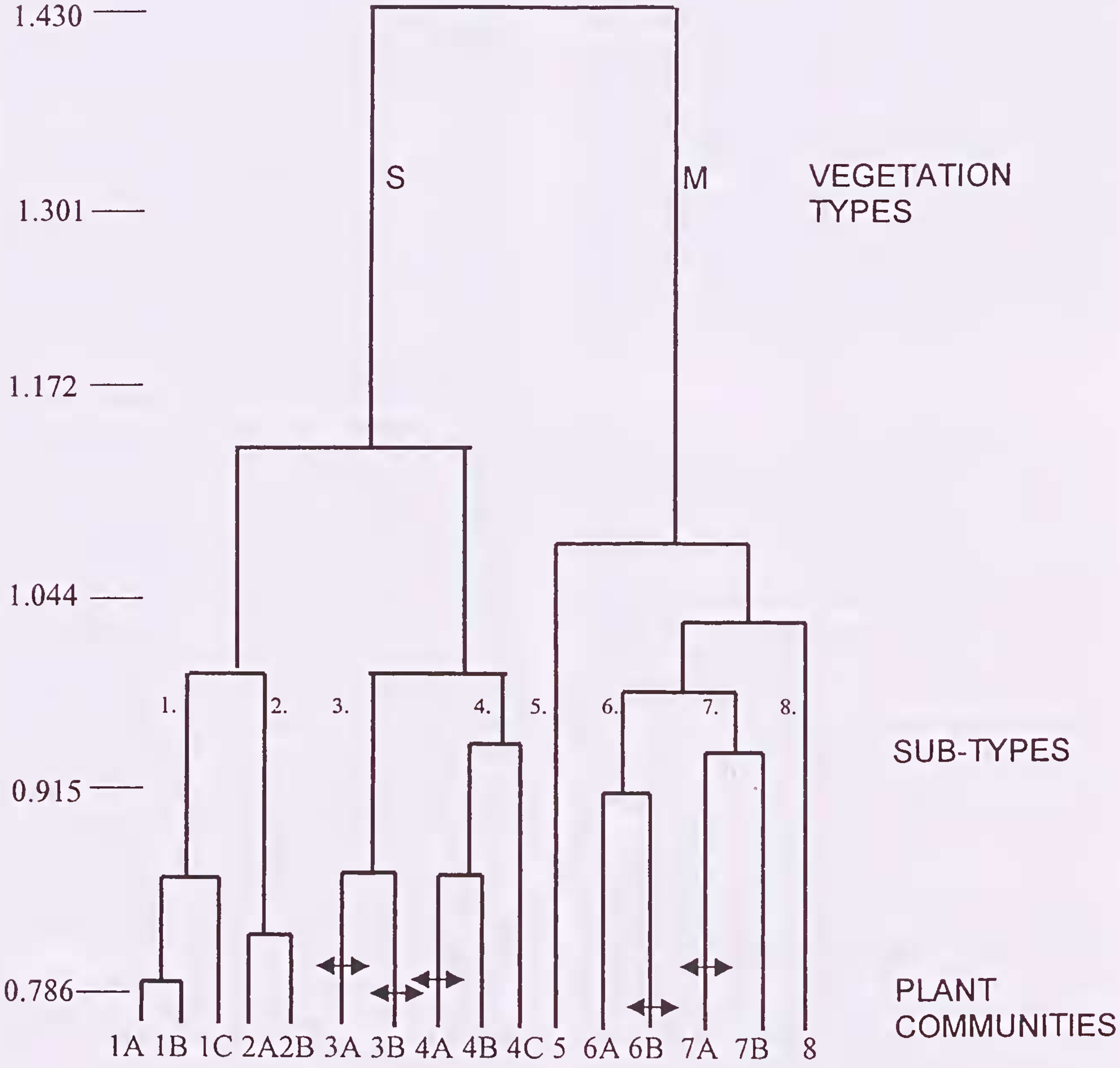

Figure 2. Partial dendrogram of the UPGMA classification of sites showing relationships between the 16 plant communities, 8 subtypes and 2 broad vegetation types. (N.B. The full dendrogram was originally cut at the 21 group level. Following fusion of adjacent groups, this number was reduced to 16. The positions of the original splits are shown on the dendrogram using arrows).

Table 1

Characterisation of plant communities in terms of dominant species in order of importance value (IV) with only species with IV of 5 or above listed. Key to genera as per text.

1A	1B	1C	2A
T. wiseana 96	*T. basedowii* 117	*T. brizoides* 102	*T. basedowii* 123
T. basedowii 45	*T. wiseana* 57	*E. leucophloia* 30	*E. gamophylla* 28
T. brizoides 27	*E. leucophloia* 24	*T. wiseana* 23	*T. wiseana* 24
E. leucophloia 21	*A. adoxa* 19	*T. basedowii* 19	*T. pungens* 19
A. marramamba 14	*A. maitlandii* 12	*S. g.* subsp. *glutinosa* 13	*A. caricinus* 16
S. g. subsp. *pruinosa* 10	*A. hilliana* 10	*A. maitlandii* 13	*A. contorta* 6
T. pungens 9	*C. hamersleyana* 7	*E. mucronata* 9	*S. a.* subsp. *oligophyllaX helmsii* 5
A. atkinsiana 8	*S. g.* subsp. *glutinosa* 5	*P. clementii* 8	
K. velutina 7		*A. caricinus* 7	
A. pruinocarpa 7		*Sida* aff. *filiformis* 5	
E. mucronata 6			
A. maitlandii 6			
S. g. subsp. *glutinosa* 6			

2B	3A	3B	4A
T. basedowii 196	*T. wiseana* 117	*T. wiseana* 93	*T. wiseana* 128
T. wiseana 28	*T. longiceps* 60	*A. xiphophylla* 49	*E. kingsmillii* 31
E. leucophloia 12	*E. trivalvis* 22	*T. longiceps* 32	*A. caricinus* 14
A. stowardii 8	*M. eleuterostachya* 15	*M. georgei* 16	*E. leucophloia* 11
S. g. subsp. *glutinosa* 6	*E. socialis* 10	*A. aneura* 15	*G. polyzygum* 9
A. bivenosa 5	*Heliotropium* sp. 7	*A. stowardii* 9	*Goodenia stobbsiana* 8
S. a. subsp. *oligophylla X helmsii* 5		*S. a.* subsp. *artemisioides* 8	*A. ancistrocarpa* 8
		A. victoriae 8	*Dampiera 'anonyma'* 7
		S. a. subsp. *helmsii* 7	*E. mucronata* 7
		Enneapogon caerulescens 7	*T. bitextura* 6
		Maireana sp. #1 5	*A. acradenia* 7
			O. xerophila 5

4B	4C	5	6A
T. wiseana 188	*A. aneura* 77	*T. melvillei* 149	*A. aneura* 36
T. pungens 18	*T. wiseana* 54	*A. aneura* 44	*A. contorta* 29
A. inaequilatera 11	*D. viscosa* 17	*T. wiseana* 15	*Mai. villosa* 20
E. leucophloia 8	*E. latrobei* 10	*A. pruinocarpa* 9	*C. fallax* 19
A. bivenosa 7	*E. muconata* 10	*C. deserticola* 7	*E. polyphyllus* 15
S. enchinocarpa 7	*A. ayersiana* 9	*E. forrestii* 6	*T. triandra* 13
P. rotundifolius 6	*T. triandra* 9	*Eragrostis dielsii* 5	*T. pungens* 12
E. muconata 6	*P. obovatus* 9	*T. pungens* 5	*A.* aff. *exoneuum* 11
T. brizoides 5	*M. villosa* 8		*E. aurea* 11
S. g. subsp. *glutinosa* 5	*Sida* sp. #6 8		*E. 'lanceolata'* 10
P. obovatus 5	*A. rhodophloia* 6		*Sida fibulifera* 10
Petalostylis labicheoides 5	*S. g.* subsp. *X luerssenii* 6		*Ab. otocarpum* 8
	S. viminale 6		*E. caerulescens* 7
	R. eremaea 6		*E. xerothermica* 7
	T. pungens 5		*E. victrix* 6
	Erempohila sp. #2 5		*P. clementii* 6
	S. g. subsp. *glutinosa* 5		*P. obovatus* 6
			P. muelleri 5

6B	7A	7B	8
A. aneura 85	*T. triandra* 50	*T. triandra* 51	*E. aurea* 142
T. melvillei 42	*E. aurea* 31	*T. pungens* 27	*A. aneura* 47
C. fallax 23	*T. pungens* 28	*A. citrinoviridis* 30	*E. victrix* 40
T. triandra 20	*E. xerothermica* 29	*E. victrix* 18	*M. florulenta* 33
P. obovatus 19	*T. wiseana* 25	*E. camaldulensis* 22	*T. triandra* 8
A. citrinoviridis 6	*T. melvillei* 11	*D. forrestii* 9	*C. fallax* 7
D. australasicus 6	*A. dictyophleba* 7	*Porana commixta* 8	*A. contorta* 7
E. 'lanceolata' 5	*K. velutina* 6	*E. benthamii* 7	
E. benthamii 5	*A. bivenosa* 5	*P. clementii* 6	
		D. australasicus 6	
		I. monophylla 6	
		Sclerolaena cornishiana 5	
		S. lasiophyllum 5	
		A. bivenosa 5	

hereafter referred to as *plant communities*. The dendrogram was also cut at the two group level to distinguish broad *vegetation types* (i.e., vegetation type 'S' and vegetation type 'M') and at the eight group level to distinguish *vegetation subtypes*. Although the determinations of cut levels and group unions were ultimately subjective, choices were guided by homogeneity analysis (i.e where average group homogeneity begins to plateau as more groups are defined by the classification; see Pressey & Bedward 1991; Bedward *et al.* 1992), the shape of the dendrogram (e.g. cuts occurred at distinct gaps in the hierarchy), and the desire to ensure that sites grouped together had a reasonable consistency in terms of dominant and common species.

The names and descriptions of the 2 vegetation types, 8 subtypes and 16 plant communities so derived follow. Dominant and indicator species for each community are shown in Tables 1 & 2, respectively.

Vegetation type 'S': hummock grassland with emergent trees & shrubs

This vegetation type dominates the upland ridges, hills and mountains as well as the pediment slopes. It is dominated by various species of hummock grasses of the genus *Triodia*, colloquially known as "spinifex" (Jacobs 1992). The genus is endemic to Australia and dominates large parts of the arid northern Australia. Hummock grasslands are rarely 'pure' grasslands as scattered trees and/or tall shrubs are usually present. Under some classification schemes (e.g. Specht 1981), these formations would be described as woodland or open woodland, but the term hummock grassland is preferred given the low cover of trees. In the study area, these trees and shrubs typically cover 5–10% and are chiefly of the genera *Eucalyptus*, *Acacia* and *Senna* (syn. *Cassia*). Hummock grasses themselves typically cover 20–25% of the soil surface.

Subtype 1: Hummock grassland with emergent *Eucalyptus leucophloia* on ridge, mountain and hill slopes

Community 1A: *Triodia wiseana* – *T. basedowii* hummock grassland with emergent *Eucalyptus leucophloia* and tall *Acacia* shrubs (on Marra mamba ridges and slopes; 9 sites).

T. wiseana dominates this community, but is often mixed with *T. basedowii*. *E. leucophloia* (snappy gum) is the dominant tree at around 5% cover. Tall *Acacia* shrubs and small trees such as *A. marramamba* (indicator species and seemingly restricted to this geological substrate), *A. atkinsiana* (also an indicator species), *A. maitlandii*, *A. pruinocarpa*, *A. hamersleyensis*, *A. pyrifolia* and, in places, *A. aneura s.l.* are scattered throughout and sometimes form distinctive groves along the contour on less steep slopes. Shrubs, including *Senna glutinosa* subsp. *pruinosa*, *S. glutinosa* subsp. *glutinosa* and *Keraudrenia velutina* subsp. *'elliptica'* ms, form a very sparse, low-shrub layer. Grasses such as *Eriachne mucronata*, *Eragrostis eriopoda* and *Paraneurachne muelleri* are occasionally found between the hummocks, but herbs and subshrubs are rarely found (Tables 1 & 3) except in the first 1–3 years following fire (pers. obs.).

Community 1B: *Triodia basedowii* – *T. wiseana* hummock grassland with emergent *Eucalyptus leucophloia*, *Corymbia hamersleyana* and low *Acacia* shrubs. (on Brockman ridges and slopes;13 sites).

This community is similar to community 1A in terms of structure and dominant species (although *T. basedowii* is often the most common species in the hummock grass mix). The major difference is the suite of shrubs present. Here small shrubs, such as *A. adoxa* and *A. hilliana*, dominate a sparse, low shrub layer (3–4% cover), with a tall shrub layer virtually absent (although *A. maitlandii* can be locally common). Another distinction from 1A is the bloodwood tree *C. hamersleyana* being a sparse but regular feature of the upper stratum. Subshrubs (small, predominantly non-woody shrubs such as *Sida* spp., *Stemodia grossa*, *Goodenia* spp.) are again uncommon in this community (Tables 1 & 3), yet are generally distinct from those of community 1A, with only one of twenty species common to both communities (namely *Abutilon otocarpum*).

Community 1C: *Triodia brizoides* hummock grassland with emergent *Eucalyptus leucophloia* (on shallow, skeletal soils on slopes and ridges; 7 sites)

Although also structurally similar to 1A, this community is dominated by *T. brizoides* (20–25% cover), a species which seems able to tolerate the shallow, skeletal soils found around outcrops of bedrock and on steeper slopes. Other perennial grasses such as *E. mucronata*, *Paspalidium clementii*, *Triodia bitextura* and *Amphipogon caricinus* are also present, particularly in the interstices of rocks and outcrops. Shrubs are less common than in communities 1A and 1B, the most common being *S. glutinosa* subsp. *glutinosa*, *A. maitlandii* and *Dodonaea coriacea* (the latter is an indicator species; Table 2).

Subtype 2: Hummock grassland of *Triodia basedowii* on pediment slopes.

Community 2A: *Triodia basedowii* hummock grassland with emergent *Eucalyptus gamophylla* mallee (on lower to middle pediment slopes; 17 sites).

The gentle pediment slopes (of around 1–3°) have shallow soils (20–30 cm deep) and are covered with small pebbles forming an ironstone pavement. Here the hummock grassland is dominated by *T. basedowii* and the mallee *E. gamophylla* is the dominant and characteristic emergent. No trees are found with the exception of *Hakea lorea* and *C. deserticola* at low densities. There is little development of a shrub layer (only ~2% cover) with the main species being the hybrid *Senna artemisioides* subsp. *oligophylla* x subsp. *helmsii*, *Bonamia rosea* and *Indigofera monophylla*. *Acacia* shrubs (such as *A. stowardii* and *A. ancistrocarpa*) occur but are relatively sparse. Semi-perennial grasses are fairly common between hummocks at some sites.

Community 2B: *Triodia basedowii* hummock grassland with emergent *Eucalyptus leucophloia* and mixed *Acacia* and *Senna* shrubs (on upper pediment slopes; 12 sites).

Again *T. basedowii* is the dominant hummock grass and species present. A very low density of *E. leucophloia* occurs mixed with leguminous shrubs and small trees

Table 2

Characterisation of plant communities in terms of indicator species in order of indicator value (%) as calculated using the procedure of Dufrene & Legendre (1997), with only species with indicator value above 15% or top ten listed.

1A	1B	1C	2A
A. marramamba 65 *S.g.*subsp.*pruinosa* 38 *A. atkinsiana* 36 *H. lorea* 20 *Eremophia* aff.*compacta* 19 *K. velutina* 16 *E. leucophloia* 16 *A. hamersleyensis* 15 *H. coatsii* 15	*A. adoxa* 63 *A. hilliana* 50 *A. maitlandii* 26 *C.hamersleyana* 25 *T. basedowii* 22 *E. leucophloia* 17 Unknown sp#4 16 *Grevillea wickhamii* 15	*T. brizoides* 73 *D. coriacea* 43 *S.g.*subsp. *glutinosa* 28 *T. bitexura* 26 *E. leucophloia* 19 *Gossypium robinsonii* 16	*E. gamophylla* 56 *T. basedowii* 24 *Sclerolaena parvifolia* 24 *C. deserticola* 21 *B. rosea* 18
2B	**3A**	**3B**	**4A**
T. basedowii 39	*M.eleuterostachya* 67 *E. trivalvis* 67 *E. socialis* 56 *T. longiceps* 28 *Heliotropium* sp. 22 *A. victoriae* 19	*A. xiphophylla* 59 *E. cuneifolia* 57 *M. georgei* 51 *A. victoriae* 40 *Maireana* sp.#1 38 *Sida* aff.*kingii* 24 *E.caerulescens* 24 *Sclerolaena* sp.#1 20 *Eremophila* aff.*freelingii* 20 *Templetonia* aff.*egena* 20	*E. kingsmillii* 69 *G. polyzygum* 44 *A. acradenia* 40 *G. stobbsiana* 35 *A. caricinus* 28 *C. ambiguus* 23 *Corchorus* sp.'*Hamersley*' 20 *Acacia spondylophylla* 20 *Dampiera anonyma* 19 *O. xerophila* 18
4B	**4C**	**5**	**6A**
A. inaequilatera 22 *T. wiseana* 19 *P. rotundifolius* 15	*S. viminale* 78 *E. latrobei* 65 *D. viscosa* 60 *A. ayersiana* 30 *Cheilanthes lasiophylla* 30 *S.g.*subsp.*luerssenii* 25 *Psydrax suaveolens* 24 *R. eremaea* 24 *A. aneura* 24 *E. fraseri* 20	*T. melvillei* 70 *C. deserticola* 27 *R. linearis* 18 *E. forrestii* 16 *Psydrax attenuatum* 15 *A. pruinocarpa* 15	*A. otocarpum* 76 *A.contorta* 70 *E. polyphyllus* 59 *M. villosa* 58 *Convolvulus* aff.*remotus* 57 *A.* aff.*exonemum* 52 *S. fibulifera* 50 *Boerhavia* sp. 46 *Abutilon* sp.#1 43
6B	**7A**	**7B**	**8**
P. obovatus 31 *A. aneura* 27 *Maireana tomentosa* 26 *C. fallax* 25 *T. melvillei* 18 *Enchylaena tomentosa* 17 *Eragrostis falcata* 17 *D. australasicus* 15	*E. xerothermica* 52 *A. dictyophleba* 44 *A. validinervia* 31 *T .triandra* 30 *A. colei* 15	*E. camaldulensis* 98 *R. kempeana* 75 *A. citrinoviridis* 62 *S. cornishiana* 55 *D. forrestii* 50 *P. maderaspatensis* 50 *Evolvulus alsinoides* 45 *I. monophylla* 42 *T .triandra* 35 *P. labicheoides* 32	*M. florulenta* 96 *E. auraea* 82 *E. victrix* 57 *A. aneura* 15

such as *A. bivenosa*, *A. stowardii*, *S. artemisioides* subsp. *oligophylla* x subsp. *helmsii*, *A. pruinocarpa*, *A. ancistrocarpa* and *S. glutinosa* subsp. x *luerssenii*. These latter species occur in other communities, but are typically more common here. The species diversity is significantly lower here than in most other hummock grassland communities and the tree and shrub cover is relatively small (Table 3). Floristically and structurally, this community is intermediate between 1A/1B and 2A.

Subtype 3: Hummock grassland and mixed *Acacia* woodland on calcareous, alkaline soils.

Community 3A: *Triodia wiseana* – *T. longiceps* hummock grassland with emergent *Eucalyptus trivalvis* – *E. socialis* mallee (on Oakover and dolomite flats/undulating land; 9 sites).

This community comprises a mosaic of the two hummock grass species (again 20–25% total cover) with

Table 3

Comparison of plant communities in terms of mean species richness and diversity, mean homogeneity, and cover (%) for all perennial and semi-perennial species and for various life-forms. Standard errors in parentheses. Test statistics refer to results of one-way ANOVA or Kruskal-Wallis test. 'Outstanding' refers to communities which were significantly different from the majority of ther communities according to relevant pair-wise comparison test. Probability levels: *: $p<0.5$; ** $p<0.1$; ***:$p<0.001$. (# richness and diversity measures do not include annual species for reasons outlined in the text).

COMMUNITY	1A	1B	1C	2A	2B	3A	3B	4A	4B	4C	5	6A	6B	7A	7B	8	Test Stat.	Prob.	Outstanding
Species Richness#	16.7	14.2	17.7	15.0	9.4	12.3	13.6	14.7	14.2	18.3	12.6	32.6	15.9	18.4	32.3	5.5	c2=44.4	***	2B,6A,7B,8
	(2.0)	(0.8)	(1.8)	(1.6)	(0.8)	(1.5)	(3.4)	(1.5)	(1.7)	(1.9)	(1.6)	(5.5)	(1.7)	(2.4)	(5.4)	(0.5)			
Species Diversity#	0.84	0.77	0.87	0.83	0.54	0.69	0.85	0.84	0.70	1.00	0.71	1.21	0.87	0.91	1.24	0.48	c2=57.8	***	2B,6A,7B,8
	(0.07)	(0.03)	(0.06)	(0.05)	(0.05)	(0.06)	(0.11)	(0.07)	(0.07)	(0.08)	(0.05)	(0.08)	(0.07)	(0.07)	(0.10)	(0.01)			
Eveness Index#	0.65	0.64	0.66	0.64	0.51	0.61	0.72	0.68	0.59	0.78	0.60	0.82	0.72	0.70	0.81	0.65	c2=58.6	***	2B,6A,7B,4C
	(0.04)	(0.03)	(0.03)	(0.02)	(0.03)	(0.03)	(0.04)	(0.05)	(0.04)	(0.04)	(0.03)	(0.01)	(0.03)	(0.03)	(0.03)	(0.04)			
No. Rare Species#	0.4	0.4	1.2	0.5	0.08	1.7	2.0	3.5	0.8	1.6	0.4	2.4	1.7	1.4	4.3	0	c2=50.1	***	7B,4A,6A
	(0.3)	(0.2)	(0.7)	(0.2)	(0.08)	(0.3)	(1.1)	(1.5)	(0.2)	(0.9)	(0.2)	(0.9)	(0.6)	(0.6)	(1.0)				
No. Common Species#	13.0	11.3	12.1	12.7	8.4	5.4	7.8	7.8	9.9	9.2	7.8	14.3	8.0	10.1	11.5	2.5	c2=63.1	***	6A,2A,1A,1C
	(2.1)	(0.7)	(1.2)	(0.9)	(0.9)	(1.0)	(1.1)	(0.9)	(1.2)	(1.3)	(0.9)	(1.8)	(1.2)	(1.2)	(1.3)	(0)			
Total Cover	35.3	37.5	35.3	28.2	29.6	30.3	24.3	22.3	37.7	37.2	27.1	48.5	27.6	42.0	42.0	32.1	*F*=2.7	**	6A, 7A
	(2.9)	(2.5)	(1.7)	(2.0)	(4.1)	(4.5)	(4.0)	(3.9)	(2.3)	(3.7)	(2.9)	(9.9)	(4.8)	(4.5)	(9.0)	(4.0)			
Tree Cover	5.0	5.7	7.3	5.5	3.8	5.8	11.3	7.3	2.7	23.9	6.5	15.2	16.3	9.1	17.4	17.5	*F*=6.5	***	4C,6B,6A,7B,4B
	(2.0)	(0.5)	(1.2)	(0.7)	(1.4)	(2.1)	(3.0)	(1.7)	(0.8)	(4.4)	(0.9)	(3.5)	(3.8)	(3.1)	(3.8)	(9.4)			
Shrub Cover	4.0	4.2	2.7	2.0	1.2	2.6	2.5	4.2	1.2	5.1	1.7	2.5	1.6	3.2	5.1	3.2	*F*=1.8	ns	nil
	(0.7)	(0.8)	(0.5)	(0.6)	(0.2)	(0.4)	(0.9)	(0.9)	(0.3)	(1.1)	(0.4)	(0.6)	(0.6)	(1.2)	(4.0)	(2.8)			
Herb/Subshrub Cover	0.5	0.5	0.9	0.8	0.24	0.8	1.3	1.2	0.9	3.6	0.6	13.0	2.2	1.4	3.6	1.2	*F*=8.5	***	6A,4C
	(0.1)	(0.1)	(0.3)	(0.1)	(0.08)	(0.2)	(0.6)	(0.7)	(0.3)	(1.0)	(0.1)	(5.0)	(0.8)	(0.5)	(1.0)	(0.05)			
Creeper/Climber Cover	0.4	0.2	0.2	0.9	0.2	1.7	0.2	0.2	0.4	2.0	0.9	2.0	1.5	1.3	2.9	0	*F*=2.0	ns	nil
	(0.2)	(0.1)	(0.1)	(0.3)	(0.1)	(1.1)	(0.1)	(0.1)	(0.2)	(0.4)	(0.3)	(0.8)	(0.7)	(0.6)	(0.4)				
Succulent Cover	0.3	0	0.7	0.3	0	1.2	3.2	0	0.1	3.6	0.8	5.1	1.4	0.2	2.2	0	*F*=7.2	***	3B,4C,6A,7B
	(0.2)		(0.3)	(0.2)		(0.9)	(1.8)		(0.07)	(1.9)	(0.5)	(2.0)	(0.6)	(0.1)	(0.8)				
Grass Cover	25.9	27.1	24.3	20.1	24.7	21.7	9.2	9.7	32.5	4.6	19.0	17.6	7.6	26.7	16.2	11.5	*F*=6.8	***	6B,4C,3B,4A,4B
	(2.6)	(1.9)	(1.8)	(1.4)	(3.5)	(4.1)	(2.6)	(2.3)	(5.4)	(1.1)	(2.2)	(4.0)	(3.3)	(2.9)	(6.5)	(3.7)			
Homogeneity	0.33	0.37	0.24	0.24	0.33	0.16	0.17	0.24	0.20	0.24	0.25	0.28	0.21	0.15	0.28	0.73	_	_	_
No. of Sites	9	13	7	17	12	9	5	7	8	5	13	7	12	8	4	2	_	_	_

emergent and characteristic mallee eucalypts such as *E. trivalvis*, *E. socialis* and, less commonly, *E. repullulans*. Average mallee cover is around 5%. *Melaleuca eleuterostachya* is by far the most common and characteristic shrub species present, with others such as *Heliotropium* sp. and *A. bivenosa* also found. This community was found on basic soils derived from calcareous parent rocks of the tertiary Oakover formation and older dolomites and shales such as those which predominate on the Jerrinah formation.

Community 3B: *Triodia wiseana* hummock grassland with emergent *Acacia xiphophylla* and other *Acacia* spp. (on dolomitic and volcanic slopes and ridges; 5 sites).

As with 3A, *T. wiseana* dominates this community. However the distribution of the grass is more patchy here as it gives way to relatively dense stands of *A. xiphophylla* (snakewood) and other acacias such as *A. stowardii*, *A. victoriae* and *A. aneura*. Dense stands of *A. xiphophylla* typically occur below major outcrops of calcrete bedrocks (breakaways) and are often mixed with *A. aneura*. The other acacias are found on more gentle slopes where the vegetation also typically contains numerous chenopod species, particularly of the genera *Maireana* and *Sclerolaena*. Considerable site to site variation in species composition was evident within this community with low homogeneity recorded (Table 3). Indicator species in addition to *A. xiphophylla* include *Eremophila cuneifolia*, *M. georgeii* and *A. victoriae* (Table 2). This community was found predominantly in the south-west of the study area where the geology and topography is more complex than elsewhere and includes outcrops of and soils derived from dolomites, dolerites, quartzites, basalts, shales and cherts, and sandstones. Further sampling of this community type is recommended to determine if it should be divided into 2 types: 1) snakewood woodland on slopes below calcrete outcrops; and 2) mixed *Acacia* and chenopod shrubland on very alkaline soils.

Subtype 4: Hummock grassland of *Triodia wiseana* with *Acacia aneura* or no/few emergent trees on a range of upland soils and landforms.

Community 4A: *Triodia wiseana* hummock grassland with emergent *Eucalyptus kingsmillii* low mallee (on mountain tops; 7 sites).

Eucalyptus kingsmillii is a small mallee characteristic of the summits of tall mountains of the Hamersley Ranges. Almost all mountain tops above approximately 1000 m have this community and it is rarely found at lower altitudes. *T. wiseana* is dominant, although *T. bitextura* is common at one site. Other eucalypts, such as *E. leucophloia* and *E. ewartiana* are found, but are sparse. Other common species vary with location; *Acacia acradenia*, *Gompholobium polyzygum*, *A. ancistrocarpa*, *Olearia xerophila* and *Hibbertia glaberrima* are examples of locally common indicator shrubs (Table 2). *Callitris glaucophylla* (cypress pine) is a fire sensitive tree found on steep slopes and other fire-excluded sites and is relatively common around mountain summits.

Community 4B: *Triodia wiseana* hummock grassland with emergent, sparse *Acacia inaequilatera* and *Eucalyptus leucophloia* (on volcanic formations; 8 sites).

This is another community dominated by the hummock grass *T. wiseana*. This community forms largely treeless hummock grassland; it has the lowest tree cover of all communities (Table 3). Trees, where present, are very sparse, with *A. inaequilatera* being the most widespread and common with an average of only 1.1% cover. In some areas very sparse *E. leucophloia* trees also occur. The shrub layer is also sparse and mainly consists of acacias such as *A. bivenosa*, *A. tetragonophylla* and *A. stowardii* and subshrubs such as *Ptilotus obovatus*, *P. rotundifolius*, *Sida echinocarpa* and *Solanum lasiophyllum*. This community was mostly found on extensive volcanic plains. Volcanic formations of the study area are varied and include dolerite intrusions (such as the Weeli-Wooli formation) to more extensive areas of older (Archaean) basalts. Where outcropping of the volcanic rock is marked, other perennial grasses (particularly *T. pungens*, *Cymbopogon ambiguus* and *Themeda triandra*) are typically found in the interstices of rocks and boulders together with more specialised species such as *Brachychiton gregorii*, *Hibiscus* aff. *coatsii* and *H. sturtii*. Two sites not on volcanics were classified in this community probably because they were dominated by *T. wiseana*. These were a mountain top site (without the usual *E. kingsmillii*, but with low density of *E. leucophloia*) and a site on calcareous soils of the Jerrinah formation with scattered *A. bivenosa* shrubs.

Community 4C: *Acacia aneura* woodland over *Triodia wiseana* hummock grass (on steep, scree slopes; 5 sites).

This community comprises dense stands of *A. aneura* (20–30% cover) over patchy *T. wiseana* and other perennial grasses such as *T. triandra* and *E. mucronata*. Broad leaved mulga (*A. ayersiana)* is also found. Subshrubs such as *P. obovatus*, *Maireana villosa*, *Rhagodia eremaea* and *Sida* spp. are relatively common. A range of indicator shrub species is also found, including *Eremophila latrobei*, *Dodonaea viscosa*, *Sarcostemma viminale* subsp. *australe* and *A. rhodophloia* (Table 2). This community is found on the steeper slopes of mountains and ridges where scree of ironstone formation covers the surface.

Vegetation type 'M': mulga woodlands with grassy understorey on alluvial flats, fans and drainage lines.

Mulga (*Acacia aneura s.l.*) dominates many of the plant communities of the valley systems within the Hamersley Ranges and is found, albeit at lower densities, in most of the other communities in low-lying areas. These areas typically feature the accumulation of fine alluvial soils washed down from the surrounding mountains and hills. Mulga woodlands are common vegetation types across the southern half of Australia's arid/semi-arid zones. *A. aneura* reaches its northern limit just north of the Hamersley Ranges (Beard 1975).

Community 5 (also *Subtype 5*): *Triodia melvillei* hummock grassland with emergent *Acacia aneura* (on upper to mid bajada slopes; 13 sites).

This community is characterised by dense hummock grass (*T. melvillei*) under a patchy stratum of *A. aneura* trees/shrubs. The density and cover of mulga is highly variable, but averages around 5–6%. Research in the study area (e.g. Start 1986; van Leeuwen *et al.* 1995) and personal observations suggest that this density is controlled by fire, with the relatively fire-sensitive mulga increasing in density with time without fire. Structurally, therefore, this community varies from a hummock grassland (with emergent mulga) to an open woodland of mulga. Other reasonably common tree and shrub species include: *A. pruinocarpa*, *Eremophila forrestii* and *C. deserticola*. This community occurs on the very slight slopes of the bajadas and other areas of alluvial fans. The soils are relatively shallow (20–40cm deep) and are reported to be underlain by a siliceous hardpan (Lorimer 1991).

Subtype 6: Woodland of *Acacia aneura* on broad drainage flats and lines.

Community 6A: *Acacia aneura* woodland/open woodland with tussock grass understorey (on alluvial flats and broad drainage lines; 7 sites).

The woodland is relatively dense (> 15% cover) and is dominated by mulga, although it is sometimes mixed with sparse eucalypts such as *E. victrix* (on broad alluvial flats and basins) and *E. xerothermica* (on broad drainage lines). Tussock and bunch grasses, most of which are perennial, dominate the ground layer. Typically many grass species are found at each site, with the number increasing following large rainfall events. Examples of tussock grass include *Chrysopogon fallax*, *T. triandra*, *P. muelleri* and *Eulalia aurea*. Subshrubs are also common and average 13% coverage. Common subshrubs include *M. villosa*, *Abutilon* aff. *exonemum*, *A. otocarpum*, *Erempohila 'lanceolata'* ms (low woody shrub), *P .obovatus and Rhagodia eremaea*. Many of these have high indicator values (Table 2). Species richness and diversity are significantly higher than in most other communities, as are numbers of common and uncommon species (Table 3).

Community 6B: *Acacia aneura* woodland/open woodland with *Triodia melvillei* – tussock grass_understorey (on outwash plains, lower bajadas and broad drainage lines; 12 sites).

This community is similar in several respects to 6A; the main differences being the dominance of hummock grass (*T. melvillei*) in the ground layer and the occurrence of *A. citrinoviridis* and *A. pruinocarpa* in the tree layer. The community is typically found on lower parts of bajadas and outwash fans. The community appears floristically and structurally intermediate between types 5 and 6A and may well represent a transitional zone or ecotone between them. On extensive outwash plains this community often exhibits a grove-intergrove vegetation pattern (Mabbutt & Fanning 1987), known in other countries as tiger bush or vegetation arcs.

Subtype 6: Woodland of *Eucalyptus* spp. on confined drainage lines.

Community 7A: *Eucalyptus xerothermica* open woodland with *Themeda triandra* – *Eulalia aurea* / *Triodia pungens* understorey (within drainage lines; 10 sites).

Scattered *E. xerothermica* trees of 5–10% cover characterise the overstorey of this community, with the occasional *Corymbia semiclara*, *A. aneura* and *E. victrix* also found. It is typically found within distinct drainage lines on subdued topographies. The understorey typically consists of either a mix of two tussock grasses (*T. triandra* and *E. aurea*) or open hummock grasses (*T. pungens* and, less commonly, *T. wiseana*). Where hummock grasses dominate, tree cover is appreciably lower. Such sites also form a distinct group in the classification. Several indicator species occur in the shrub layer; these include *Acacia dictyophleba*, *A. colei* and *A. validinervia*

Community 7B: *Eucalyptus victrix* – *E. camaldulensis* – *Acacia citrinoviridis* woodland with *Themeda triandra* – *Triodia pungens* grassy understorey (along major creeklines; 4 sites).

A mixture of *E. victrix* (coolabah) and *E. camaldulensis* (river redgum) form a tall woodland formation along the major creeklines of the study area. *A. citrinoviridis* is another relatively common tree in these areas. The ground layer is dominated by perennial grasses such as *T. triandra*, *T. pungens* and, to a lesser extent, *Eriachne benthamii*, *E. mucronata*, *P. clementii* and *P. muelleri*. Shrubs comprise around 5% cover. A large number of shrub species were found in this community; the more common ones are *Dicladanthera forrestii* (indicator species), *Dipteracanthus australasicus*, *A. bivenosa*, *A. pyrifolia*, *A. sclerosperma*, *Solanum lasiophyllum* and *I. monophylla*. Several other indicator species identified for this community include *Rulingia kempeana*, *Phyllanthus maderaspatensis* and *Dodonaea lanceolata*. Overall species richness and diversity is significantly higher than at most other sites (Table 3).

Community 8 (also Subtype 8): *Eucalyptus victrix* – *Acacia aneura* open woodland over perennial tussock and bunch grasses (in broad drainage basins; 2 sites).

There are several internal drainage basins in the study area which collect water and sediment from the surrounding hills and ranges. Where the basin is extensive, an open woodland of coolabah (*E. victrix*), variously mixed with smaller mulga trees (*A. aneura*), is found on the very fine, deep alluvium at the lowest parts of the basin. This community is floristically poor (Table 3) with only tussock grasses (such as *E. aurea*, *T. triandra*, *C. fallax*), bunch grasses (such as *A. contorta*) and the woody, much-branched shrub *Muehlenbeckia florulenta* (a characteristic species) being recorded in the understorey. As this community was only sampled in the middle of a dry period, the species richness recorded is likely to be below its potential maximum. This community is the most distinct in floristic terms (Fig 2).

The non-hierarchical classification procedure (ALOC; Belbin 1987), when forced to produce 16 groups, resulted in more-or-less the same groups, each with a very similar (sometimes identical) composition of sites to the groups resulting from the hierarchical procedure (UPGMA). The major differences between the two classifications were that ALOC: 1) divided the *T. wiseana/T. basedowii* hummock grasslands on slopes into upper slope/plateau sites and lower slope sites rather than into groups linked to geological substrate; 2) community 3B was divided into two groups, one dominated by *A. xiphophylla* and the other dominated by *A. victoriae* and chenopods; and, 3) the two coolabah-mulga woodland sites of the drainage basins (community 8) were clumped with mulga woodlands with bunch grasses (community 6A). These two coolabah-mulga sites had the lowest affinities to their group of all sites and indeed formed a separate group when the ALOC procedure was forced to produce 17 groups.

Classifications using an initial matrix of transformed species cover values rather than IVs also resulted in very similar groupings of sites to that described above, and, for most communities, their composition in terms of sites were identical. The two major differences of the dendrogram produced using cover values were: 1) community 4B contained several more sites dominated by *T. wiseana* including several which were not on volcanic plains but on hill tops and upper slopes of Brockman ironstone formation where several of the characteristic shrubs of this formation are often absent; and 2) community 7A was more clearly divided into two groups, one with the ground-layer dominated by *T. pungens* and the other by *T. triandra* and other tussock grasses. This synchrony between the two classification approaches is no doubt derived from the strong correlation between transformed IVs and cover values (r=0.87; n=190).

Analysis of similarity (ANOSIM) test, performed with 1000 random permutations, demonstrated that the 16 groups determined by the two classification procedures were always more dissimilar to each other than 16 groups randomly determined. This implies that groups determined are significantly different to one another in terms of species composition (p<0.001). Although this is expected, the ANOSIM, and the fact that two completely different classification algorithms (one hierarchical and the other not) produced very similar groupings, support the idea that "real" groupings were detected and suggest that correct decisions were made with respect to classification methodology (Belbin 1994).

Community comparisons

A comparison of structural, floristic and growth-form features are displayed in Table 3 for the plant communities. There are several significant structural differences between the various plant communities and vegetation types. Mean total cover varies from 22% on mountain tops to 42–50% on drainage lines and flats. Mulga woodland on flats (community 6A) and *E. xerothermica* woodland within drainage lines (7A) have significantly higher cover than hummock grassland communities (Table 3). Tree cover is, not surprisingly, significantly higher in woodland communities compared to communities of hummock grassland on slopes and pediments (typically 15–24% cover compared to between 4–6% cover of trees). Tree cover on volcanics (community 4B) is significantly lower on average than many other communities, including some hummock grassland ones. Grass cover is relatively high (20–30%), except in the following communities which are significantly lower than most others: mulga woodland on scree slopes (4C), snakewood woodlands (3B), hummock grassland on mountain tops (4A) and mulga – *T. melvillei* – tussock grass (6B).

Average (perennial) species richness and diversity are significantly higher within mulga woodland on flats (community 6A) and creekline *E. camaldulensis – E. victrix* woodlands (7B) than in most other communities (Table 3). In addition, far more annual/ephemeral species were sampled in plots of these two communities than in hummock grassland communities. Hummock grassland on pediments and bajada slopes (communities 2A, 2B & 5) are generally less rich and diverse than other communities. Community 8 (*E. victrix* woodland of alluvial basins) had the lowest perennial richness and diversity of all communities (Table 3); median values were significantly lower than most other communities. Diversity values, although heavily influenced by species richness, also depend on the evenness of species distribution at sites. Values of evenness are relatively similar for all communities (i.e. around 0.6–0.7), except for communities 6A and 7B which are significantly higher (i.e. more even distribution of species) and 2B which is significantly lower than most other communities (Table 3). The richness of uncommon species (those found at less than 3 sites) is significantly higher (on average) within mulga woodland on flats (community 6A), along creeklines (community 7B) and on mountain tops (community 4A) compared to many other communities (Table 3). Whilst actual numbers would depend to a certain degree on the intensity of sampling in each community, these three communities have far more uncommon species than other similarly sampled communities. The uncommon species are mainly herbs and subshrubs in the first two communities, whilst they are mostly low shrubs on the mountain tops. Species positively identified as being rare and/or poorly known (as listed by the Western Australian Department of Conservation and Land Management) were few and mainly found on mountain tops.

Communities on calcareous soils (3A & 3B), *T. wiseana* hummock grassland on volcanics (4B) and *E. xerothermica* drainage line community (7A) are much less homogeneous in terms of species composition than other communities (Table 3). Each of these communities has at least one site that is distinct in some way to all the others. For instance, community 4B includes one site containing no trees on calcareous soils which seems to be placed in this group because of shared dominance by *T. wiseana*. Community 3B includes two quite dissimilar sites dominated by *A. victoriae* and other *Acacia* shrubs, rather than *A. xiphophylla*. They are clumped with other 3B sites because of understorey similarities. Quite possibly, these four heterogeneous communities will be split into a number of quite distinctive sub-communities, given the patterns shown in the classification, but sampling has been insufficient to confirm this. Communities which were relatively homogeneous in terms of species composition are 8, 1A, 1B and 2B (Table 3).

Ordinations of sites

The three-dimensional solution provided a considerable improvement in stress over a two dimensional solution (0.18 *c.f.* 0.26) and were hence used despite the increased difficulty in displaying patterns (Fig 3). Kruskal (1964) suggests that stress values less than 0.2 should be aimed for, whilst values less than 0.1 provide a "satisfactory" goodness of fit. These however are general guidelines at best as stress values are influenced by, amongst other things, number of sites and heterogeneity of communities. Ordinations performed using cover values rather than IVs in the initial site by site matrix produced a very similar pattern of

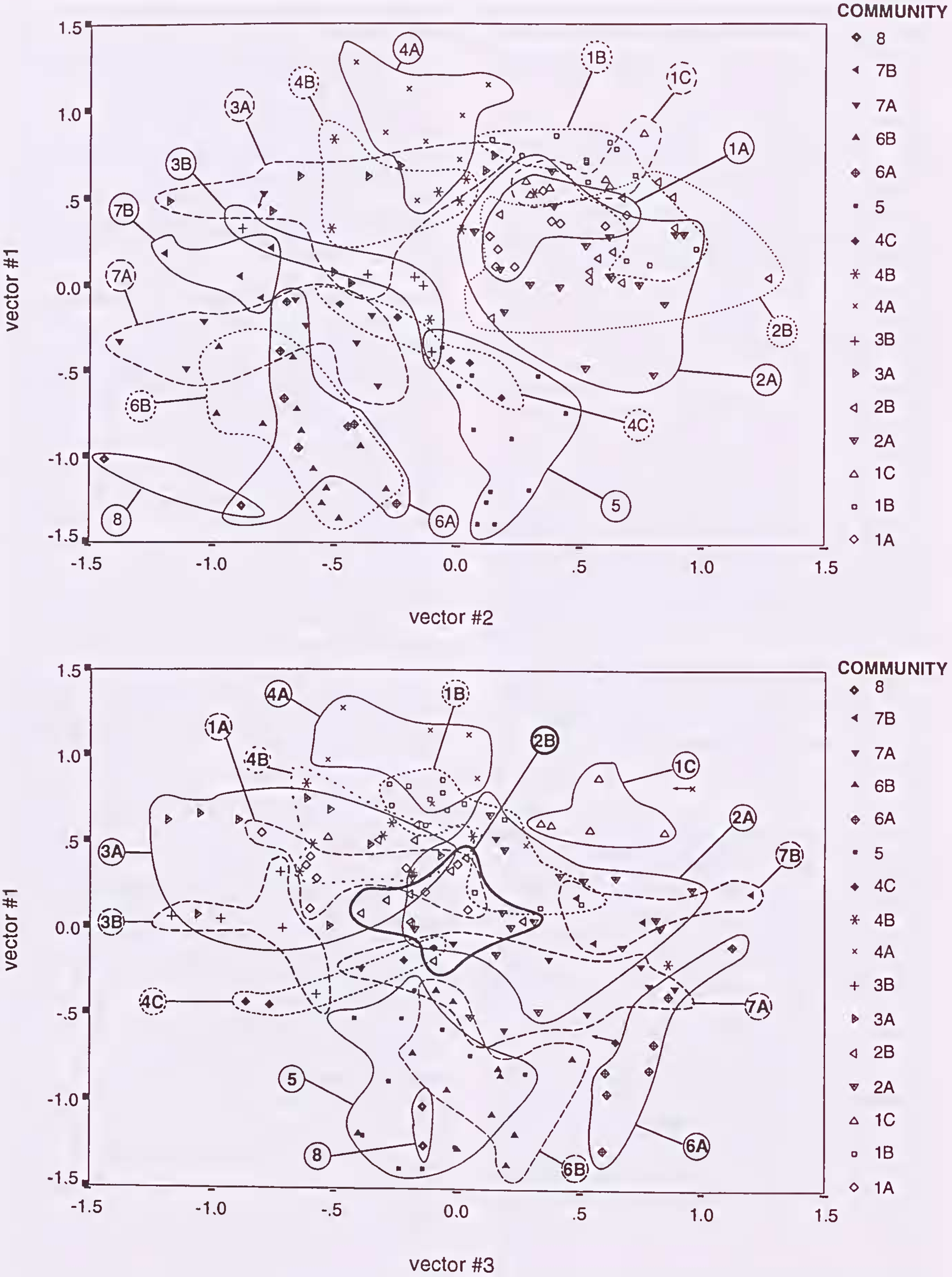

Figure 3. A 3-dimensional ordination of all sites based on all species and using SSH-MDS with the approximate space occupied by the 16 plant communities delineated: a) vectors 1 vs 2; b) vectors 1 vs 3.

communities. Procrustes rotation between the two ordinations demonstrated a very good level of fit (0.15) given the number of sites (Belbin 1994), indicating very little difference in general patterns displayed between using cover values and IVs as the initial data.

The three-dimensional ordination of all sites is displayed as two separate 2-dimensional plots (Fig 3). Sites belonging to a certain plant community generally grouped together in the ordination. Despite this general trend, the two outstanding features of the ordination plots were: 1) the considerable spread of sites within each community (reflects relatively high variability in species composition between sites within a plant community); and 2) the overlap of the ordination space occupied by a particular community with that of other communities. In other words, few discrete communities occurred. Indeed, a small number of communities clearly graded into other communities. There was also a small number of outliers (sites which are placed some distance from their respective community).

Hummock grassland at upland sites (communities 1A, 1B, 1C, 4A, 4B) were separated from the lowland communities more or less along the first vector (Fig 3). Generally the sequence of communities along this vector reflected topographic position with the mountain top community (4A) uppermost, followed by other upland communities, then pediment and bajada communities, with lowland communities at the base of this vector. Species strongly and significantly correlated to this vector were *A. aneura* (r = -0.79), *T. basedowii* (+0.74), *E. leucophloia* (+0.70), *T. triandra* (-0.67), *C. fallax* (-0.62), *E. xerothermica* (-0.51), *A. adoxa* (+0.47), *S. glutinosa* subsp. *glutinosa* (+0.41), *E. victrix* (-0.40), *M. villosa* (-0.39), *E. 'lanceolata'* (-0.36), *E. benthamii* (-0.36), *R. eremaea* (-0.36) and *C. hamersleyana* (+0.35). Of the upland communities, 1A, 1B & 1C were reasonably separate from each other along the first and third vectors (Fig 3b), however community 4B was highly variable and overlapped with each of these communities (Fig 3b), as well as communities 3A & 3B (Fig 3a). Community 4A (*E. kingsmillii* low mallee over hummock grass on mountain tops) formed a fairly distinct group along the first vector, but showed considerable variation along the third vector where it overlapped with communities 4B, 1B and 1C. The slight overlap with 1C was most likely by virtue of site E104 which is a mountain top site dominated by *T. brizoides* rather than *T. wiseana*, as is typical of community 4A. Pediment communities (2A and 2B) were not readily discernible from one another, were extremely variable and overlapped considerably with hummock grassland communities of uplands. They occupied the ordination space between the upland hummock grassland communities and the woodland communities on flats and other drainage features, although there was appreciably less overlap with the lowland communities (Fig 3). 2B was generally positioned between 2A and upland sites.

Communities on volcanics and calcareous soils (3A, 3B & 4B) were generally separated from those derived from ironstone formations along vector 3 (Fig 3b). Hummock grassland with mallee (community 3A) formed a distinguishable, albeit variable, group at the left of the plots (Fig 3). This group overlapped considerably with the community 4B group; both groups shared a dominance of *T. wiseana*, but have different dominant trees. Community 4B therefore occupied the ordination space between the calcareous and iron-formation hummock grasslands. The snakewood woodland community on calcareous soils (community 3B) formed a more discrete and less variable group than 3A, although there was some overlap.

In terms of lowlands, community 6B (mulga woodland with mixed *T. melvillei* and tussock grass understorey) occupied the ordination space between communities 5 (bajada mulga with *T. melvillei*) and 6A (mulga with tussock grass), and overlapped slightly with both (Fig 3). Mulga woodland on steep scree slopes (community 4C) formed a fairly discrete and confined group in the middle of the ordination space between the other mulga woodland communities and hummock grassland communities dominated by *T. wiseana*. The two drainage line communities (7A & 7B) separated along the first vector (Fig 3a). Community 7A overlapped considerably with mulga woodland communities, while 7B overlapped more with hummock grassland on calcareous and volcanic soils (3A & 3B; Fig 3a), as well as community 2A (Fig 3b). Sites on drainage and creek-lines seemed to be placed (in the ordination space) near to the communities which they abut in real (i.e. geographic) space. Community 8 (*E. victrix* woodland in broad drainage basins) formed the most distinct group, although it was placed near mulga woodlands.

Differential profile

The distributions of communities along the Marandoo topo-sequence are shown in the differential profile (Fig 4) with the degree of overlap between adjacent communities demonstrated in terms of species composition (vertical axis) and geographic distance (horizontal axis). A major change in species composition occurs between community 5 (*T. melvillei* hummock grassland) and communities 2A/2B (*T. basedowii* hummock grassland). The transition between 1A and 2A/2B was considerably more gradual both spatially and floristically, whilst that between 5 and 6B was relatively sharp, although it involved only a small degree of change in species composition (Fig 4). Other transitions were difficult to describe given inadequate sampling in and around the transition zones.

Discussion

This paper identifies and describes 16 plant communities within an approximately 8,000 km^2 section of the central Hamersley Ranges. Indicator species are also identified for each community. A small number of communities are distinct in terms of floristic composition, structure, species richness and diversity, whilst most are only subtly different and intergrade with other communities in respect of these parameters. The pattern of species distribution across the landscape is one of several dominant to sub-dominant species found across a wide range of communities (such as *T. wiseana*, *T. basedowii*, *A. aneura*, *E. leucophloia*, *S. glutinosa*, *P. obovatus*), with many of the other species uncommon and restricted to one or a few communities. A similar pattern of species distribution has been found in other mountainous deserts, such as Turkana, Northern Kenya (Patten & Ellis 1995), Oman (Ghazanfar 1991), central

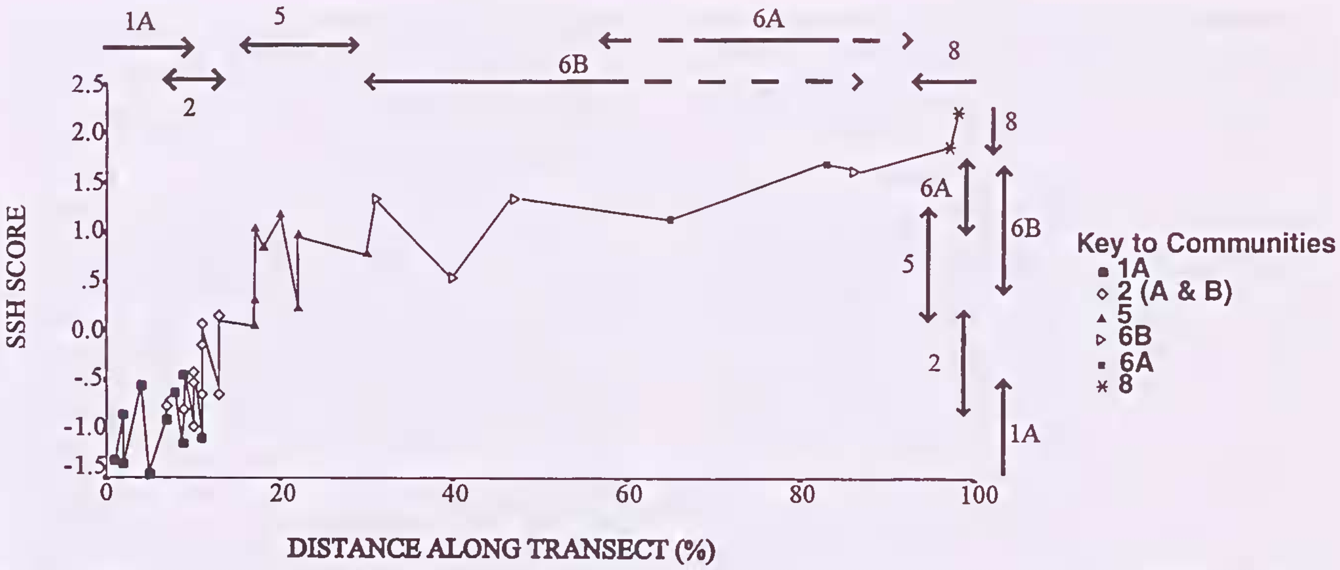

Figure 4. Differential profile showing changes in floristic composition (SSH score) with distance along a topographic profile of 35 sites located along a ridge top to valley floor catena at Marandoo. The approximate position of communities are indicated in both geographic space (horizontal axis) and ordination space (vertical axis).

Australia (Griffin 1990) and the Chihuahuan Desert of North America (Wierenga *et al.* 1987; Plumb 1991). Keighery *et al.* (2000) found certain *Acacia* species (such as *A. sclerosperma, A. tetragonophylla* and *A. linophylla*) widespread and often dominant across a range of vegetation types on red sands of the southern Carnarvon Basin. Similarly *A. aneura* dominates many recognisable plant communities in the Murchison River catchment (Curry *et al.* 1994).

Nine types of hummock grassland communities are identified on upland and piedmont slopes. These communities have very uneven species distributions as the hummock grasses (mostly either one or two of *T. wiseana, T.basedowii, T. brizoides* or *T. melvillei*) are clear dominants at most sites. Such species were highly influential in determining floristic gradients and major groupings even following severe (log) transformations. Despite this, the sub-dominant and uncommon tree and shrub species were important in determining communities within the vegetation subtypes.

A major gradient in species composition identified corresponds to the topographic sequence from hill or mountain top to valley floor (i.e. catena) typical of the northern and eastern parts of the study area where the topography consists of a series of well defined ranges and ridges of ironstone formations with intervening broad valley systems. Many of the major species of the study area are associated with this floristic gradient (e.g. *A. aneura, T. basedowii, E. leucophloia*). A sequence of communities was also recognised along such catenae. A catenary pattern of relatively distinct communities has been described many times for arid, mountainous areas (Wierenga *et al.* 1987; Cornelius *et al.* 1991; Parker 1991; Cowlishaw & Davies 1997) and has been described as a characteristic feature of such regions (Ayyad 1981). The general catenary sequence found in the northern part of the study area can be summarised as follows: i) hummock grassland (HG) with *E. kingsmillii* on mountain tops; ii) HG with *E. leucophloia* (one of three communities depending on substrate and soil) on upland slopes; iii) HG with *E. gamophylla* on pediment slopes; iv) HG with sparse *A. aneura* (mulga) on bajada slopes and outwash areas; v) mulga woodland with tussock and other grasses on alluvial flats. Large drainage basins have an additional community dominated by *E. victrix* and tussock grass below the mulga woodlands, whereas broad drainage lines, where present, have woodland of *E. xerothermica* with tussock grass understorey and major streams have tall woodland dominated by *E. victrix* and *E. camaldulensis*. It is clear from the descriptions given that several communities are strongly associated with particular geomorphological features. There is also evidence of a secondary differentiation (within landforms) by geological substrate; floristically distinct communities were found on uplands of the Marra Mamba Iron formation, Brockman Iron formation and volcanics, for instance. Relationships between vegetation patterns and environmental variables will be further explored in a subsequent paper. Vegetation studies of the greenstone and ironstone ranges of the Eastern Goldfields (Gibson *et al.* 1997; Gibson & Lyons 2001) have demonstrated the importance of soil type in determining plant communities, with much of the edaphic variation linked to catenary patterns in landform and surface geology.

Although several communities are floristically distinct, others appear to be transitional, either in spatial terms (e.g. ecotones or ecoclines) or in temporal terms (different seral or successional stages). Differential profiles enable one to simultaneously characterise the nature of transition zones in both spatial and floristic terms. In this way they have an advantage over ordinations which show patterns based on floristic similarities only. Differential profiles describe beta diversity (i.e. species turnover) along topographic gradients (Whittaker 1965; Whittaker 1972). The differential profile of a typical catena of the study area (Marandoo) shows that some communities are relatively discrete with only a narrow zone of transition with surrounding communities, whilst others clearly intergrade (spatially) with other communities. These two contrasting types of transition have often been described as ecotone and ecoclines respectively (van Leeuwen 1966; van der Maarel 1990). Hypothetically, transition types form a continuum between these two extremes (van der Maarel 1976), although Hobbs (1986) recognised 5 discrete types of transition in the field, each with their own characteristic pattern of species turnover and controlling factors. Narrow ecotones (i.e. particularly rapid spatial transitions between communities) are evident in the landscape as vegetation boundaries. Essentially two types of narrow ecotones have been recognised: *structural boundaries* where more-or-less only the dominant species of the upper stratum change dramatically (e.g. many savanna – forest boundaries) and *floristic boundaries* where there is an overall change in species composition over a short distance (Wiens *et al.* 1985; Hobbs 1986). Selective disturbance has been attributed as a cause of the first type of ecotone (e.g. the elimination of trees in part of the transition zone by disturbance), whereas the second is seen as the response of two distinct and relatively homogeneous environments meeting (van der Maarel 1976; 1990). The differential profile of this study suggests that transitions between HG communities on hill slopes and HG on upper pediments are ecoclines implying a gradual change in controlling environmental factors, although with considerable point to point variation in these factors. Such a pattern would be expected given the gradual change of slope moving from upland to pediment. The *T. melvillei* HG on bajada slopes (community 5) is spatially distinct from communities upslope and downslope. Transitions between these communities can therefore be described as narrow ecotones although each seems to of a different type. The transition with *T. basedowii* HG upslope seems to be more of a floristic boundary as there is a rapid turnover of species, whilst the transition with mulga woodland downslope (community 6B) is likely to be a structural boundary (given little change in species composition apart from the dominant species). Van Leeuwen *et al.* (1995) who studied the mulga woodlands of the study area, also recognised this distinctive *T. melvillei* HG community and postulated it was the result of recent fire within mulga woodland with hummock grass understorey on alluvial slopes. Indeed observations of burnt mulga stems in this community support this hypothesis. Van Leeuwen *et al.* (1995) felt that given sufficient time (without fire), this community would return to a mulga-hummock grass mix such as community 6B. In other words, these two communities (5 & 6B) may be successional stages of the same community. Van Etten (1988) found structural boundaries between mulga woodlands with hummock grass understoreys and hummock grassland elsewhere in the Hamersley Ranges and hypothesised that, on gradual slopes at least, they were the result of differences in fire regimes: hummock grasslands burn on a regular basis, whilst mulga communities rarely burn and contain many fire sensitive species. Mulga itself is a fire sensitive species and, although it has a limited capacity to regenerate from rootstock, it is vulnerable to repeated fires (Fox 1985; Hodgkinson 2001). Fire then is a possible cause of these structural boundaries between communities 5 and 6B. Long-term monitoring of boundaries is occurring in the study area to confirm the dynamic nature of these boundaries (A.N. Start, pers. comm.). The floristic boundary upslope of the *T. melvillei* – mulga communities suggest a distinct environmental change along the gentle pediment and bajada slopes. It is hypothesised that this change corresponds to the change from Tertiary, consolidated, colluvium deposits of the pediments with their typical ironstone pavements to more recent alluvium deposits typical of bajada and alluvial fans. Transitions between communities further downslope could not be identified because of inadequate sampling in the transition zones. Clearly there is a need to sample more intensively along catenae and to replicate studies over a variety of topographical gradients elsewhere in the study area to clarify transition types between communities and to test hypotheses generated here relating to spatial change between communities. The single catena studied here, however, demonstrates the usefulness of transects in describing vegetation patterns in real space, and that transitions between communities identified along the toposequence vary considerably in terms of width and other characteristics. Austin (1989) and Austin & Smith (1989) recommended the study of transition zones as an important adjunct to ordinations and classifications to clarify the spatial features of transitions.

In the south-western portion, geology and landform are considerably more complex compared to the ironstone ranges and intervening broad valleys elsewhere in the study area. Geological formations, which influence surface soils, comprise a range of volcanics (varying from ancient Archaean granites and gneisses to lower Proterozoic basalts to dolerite intrusions of various ages) and calcareous sedimentary deposits (Proterozoic sandstones and dolomites to Tertiary limestone/calcrete). Although three communities were recognised as existing on these substrates, they were relatively heterogeneous. As time and access constraints did not enable the full topographic and geological variation to be adequately sampled, there remains a strong likelihood that more communities can be defined in the southern half of the study area. One possible community is *A. victoriae* – *A. bivenosa* open shrubland (with chenopods) on calcareous flats. Mulga communities with understoreys different from that described here (e.g. dominated by *T. pungens* and *Eremophila fraseri*) are known for volcanic uplands of the area. Greater sampling is recommended for this portion of the Hamersley Ranges. Furthermore, a number of known landform types were not sampled in the study area as they occurred in small patches/narrow bands (and therefore were beyond the scale of the study) or were not encountered. These included scarps and cliff faces, patches of cracking clays, gorges and narrow drainage lines through pediments, all of which contain a fairly discrete suite of species and, frequently, species restricted to those landforms.

The classification presented here therefore should not be regarded as a comprehensive or an ultimate account of plant communities of the Hamersley Ranges. Rather it is a preliminary classification scheme on which to build and modify as more land around the study area is sampled. Further sampling is also needed to confirm those communities which were shown to differ according to classification methodology, or were otherwise poorly sampled and/or relatively heterogeneous. Based on observations made by the author and others, the vegetation subtypes identified seem fairly ubiquitous and consistent across the region, and extension of the classification would most likely come in the form of additional communities within subtypes. A comprehensive, robust classification for the region would be of considerable benefit for those involved in conservation planning, land management and environmental impact assessment, especially if the various plant communities and other vegetation units were accurately mapped to provide information on their spatial extents and patterns (van Etten 1998). Such an extensive study of flora and vegetation will accompany the Pilbara Biological Survey which commenced in mid 2003. It is also argued that the classification methodology used here has advantages over others employed for the region as it is based on floristics (and hence seeks to maximise the variation in species composition among vegetation units), is hierarchical (and so amenable to different scales), and is based on congruence among different approaches. This latter feature would lead toward a more objective and robust classification given the wide variety of choices made in terms of cut levels, data type and transformation, classification algorithm, and the like (Legendre & Legendre 1998).

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